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Homeostatic Relationships of Single- and Double-crosses of Corn

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HOMEOSTATIC RELATIONSHIPS OF SINGLE- AND DOUBLE-CROSSES OF CORN

BY

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This thesis is approved as a creditable and independent investigation by a candidate for the degree, Doctor of Philosophy, and is acceptable as meeting the thesis requirements for this degree, but without implying that the conclusions reached by the candidate are necessarily the conclusions of the major department.

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Abstract

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Under the supervision of Professor D. B. Shank

The inherent homeostatic properties of single- and double-cross corn hybrids were studied by growing the plant materials in six locations over three years.

Measurements of plant height and ear weight were recorded and used to calculate means and variances. Variances were pooled over locations and years and confidence intervals for the variance estimates were computed by use of the chi-square method. A lower variance for an entry, when compared with other entries grown in the same environment, was considered to be the result of relatively better homeostatic properties. Comparisons of entries were made by the use of confidence intervals for the variance estimates, with overlapping of intervals indicative of no significant difference in variability.

The theory that single-cross hybrids are more variable between locations and double-cross hybrids more variable within-locations was partially substantiated. It was concluded that more diverse environmental conditions, either more locations and/or more years, would be required to more accurately detect differences in the relative homeostatic properties of the entries used.

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INTRODUCTION

The concept of utilizing hybrid vigor in field corn production was first proposed by George H. Shull in 1908, when he advocated the crossing of homozygous inbred lines to utilize the highest degree of hybrid vigor. This concept was never put into practical use, mainly because of lack of vigorous inbred lines and their poor seed production. In 1917, D. F. Jones proposed the crossing of first generation hybrids to produce double-cross hybrids and it was at this time that hybrid corn had its beginning.

The use of double-cross hybrids was originally proposed as a method of overcoming the seed production problem, but it was later found that their genetic variability was a further advantage. A double-cross population is composed of many hybrids or many genotypes, so it has greater genetic variability than a single-cross population in which all plants are genetically the same. Genetic variability between individuals causes each plant to develop in a different way so that minor environmental fluctuations will affect individuals rather than the whole population. Lerner (20) proposed the term "genetic homeostasis" to describe the ability of populations to regulate and utilize genetic variability. Jones (18) had previously proposed the term "genetic equilibrium" and Darlington and Mather (6) had used the term "genetic inertia." These three terms all refer to essentially the same concept of some type of regulatory mechanism that restricts variation within reasonable limits, while at the same time, allows an organism to adjust and adapt to changes in environment.

The use of double-cross hybrids has been an unqualified success and for some time has almost completely replaced other methods of corn breeding. However, in recent years, several seed corn companies have been advocating and selling single-cross hybrids for use by farmers for grain production. This raises the question as to the stability of such narrow genetic base hybrids under the very diverse environmental conditions that are found in South Dakota. It is quite possible that certain environmental stresses, such as drought, hot winds, high rainfall, etc., might occur when an entire population of a single-cross hybrid is at a critical stage in its development. This could result in drastic reductions in yield or even in a complete loss. Theoretically, one would expect a hybrid with a wider genetic base, such as a double-cross, to be more homeostatic because of its greater inherent genetic variability.

In an attempt to gain information on this point under South Dakota conditions, this study was conducted. It is concerned with the variation in plant height and ear weight of a selected group of single-cross and double-cross hybrids grown in different soil and climatic environments and in different years in East Central South Dakota.

REVIEW OF LITERATURE

Homeostasis, as originally used by Cannon (3) referred to the ability of an organism to maintain certain aspects of its physiology constant despite environmental forces tending to disturb their constancy. This idea of balance, maintained through co-ordination of complex physiological processes, as a necessary condition for the preservation and perpetuation of life, is an ancient one. Cannon has traced it, at least in its primitive form, back to the time of Hippocrates. He and his followers have reduced the early ideas of some mysterious and mystical property of biological organisms to terms of interactions between constituent parts and functions.

Lerner (20) proposes the term "genetic homeostasis" to define the self-equilibrating properties of Mendelian populations which tend to retain a genetic composition that produces a maximum average fitness in a particular environment. This is very probably the same property as the "genetic inertia" of Mather and Harrison (27). Lerner concludes that the most likely mechanism for genetic homeostasis lies in the superiority with respect to fitness of the heterozygous over the homozygous genotypes. Attempts to shift populations too rapidly and too far from adapted mean values for specific traits, either by artificial selection or changes in the breeding program, are counteracted by natural selection which is directed towards the maintenance of a phenotypic balance between fitness determined characters.

"Genetic stability," "genetic flexibility," "phenotypic flexibility," and "stability of the environment" are terms used by Thoday (35) to describe the factors involved in overall fitness. "Phenotypic flexibility," or the capacity of the individual to adapt to local conditions is further sub-divided into "developmental flexibility" (capacity of the individual to adapt irreversibly to local conditions) and "behavior flexibility" (capacity of the individual to adapt reversibly to local or temporary conditions).

Waddington (39) questions the use of the term "homeostasis" because it seems to imply a stationary state, whereas development essentially involves a change in time. He prefers the terms "canalization" or "buffering" which refer to an equilibrium state. Warburton (40) prefers to use "feedback" to describe the property of biological organisms to oppose deviation of a certain variable from a certain value by other controlling factors. Feedback does not imply a steady state (homeostasis) but implies the attainment of a predetermined state from widely divergent initial ones. Developmental feedback maintains the physiological balance of organs in spite of mutations tending to disturb it.

The theory of alternative pathways was proposed by Lewis (23) to account for the greater phenotypic stability of heterozygous F_1 hybrids of tomato over homozygous inbred lines. This stability is due to gene action and he proposes that a heterozygote with different alleles will have alternative pathways through which a substrate can be changed to a product. For this theory to work, he also assumes

that different genes will in general, but not always, have different optimum conditions in which they exert their influence. A change in environment may suppress one pathway but another one may still be functional so that the end result is still achieved and variability remains low.

Along a similar line, Haldane (13) postulated the presence of a complex enzyme which is presumably gene controlled by the action of one or more genes in the heterozygous state, or by nonallelic interactions (epistasis). This could be present in either heterozygotes or homozygotes but it would be assumed theoretically, that the greater number of alleles in the heterozygote would promote better homeostatic properties.

Robertson and Reeve (30) suggest that heterosis or increased size and vigor, and reduced susceptibility to environmental variations are both manifestations of the same phenomenon of heterozygosity in Drosophila melanogaster. The heterozygotes, with their greater number of alleles, will have a greater biochemical versatility (more pathways) in their developmental processes. The effects of environmental variations will thereby be lessened.

The lesser variation of heterozygotes as compared to the greater variation of homozygotes was interpreted by Yoon (41) as an expression of the better ability of heterozygotes to maintain their own consistency among varying environmental conditions. For the particular feature studied in mice, the developmental homeostatic

functions were superior in heterozygotes. Becker and Berg (2) reached the same conclusions from their investigations with chickens.

The genetics of homeostasis in Drosophila, as reported by Dobzhansky and Wallace (9), included studies of rates of survival of individuals "homozygous" and "heterozygous" for certain chromosomes. The homozygotes often showed significantly different survival rates in the varying environments of the replicate cultures and conversely, the heterozygotes gave usually uniform survival rates despite the environmental variations. Their data infer that homeostatic adjustments are superior in heterozygotes over those in homozygotes. In further studies along the same line, Dobzhansky and Levene (8) compared the buffering ability of the heterozygotes and homozygotes for certain second chromosomes of Drosophila pseudoobscura. The developmental patterns of the heterozygotes were more homeostatic (better buffered) against environmental disturbances than those of the homozygotes. There was a positive correlation between viability and homeostatic buffering while the correlation was negative between viability and environmental variances.

The relationship of heterozygosity to homeostasis in Maize hybrids was investigated by Adams and Shank (1). They found that while homeostasis was highly related to heterozygosity, highly significant differences within groups suggested that heterozygosity itself was not a sufficient explanation. The three hypotheses of alternate pathways or complex enzymes, heterozygous balance, and component

characteristics or processes were discussed. The heterozygous balance hypothesis fails to account for the differences in buffering within groups having the same level of heterozygosity. In the case of the other two hypotheses, heterozygosity appeared to promote internal adjustment at the genic or component level to manifest homeostasis.

Vetukhiv and Beadmore (38) studied the influence that environment may have on the manifestation of heterosis and homeostasis in parental lines and F_1 and F_2 crosses between geographical populations of Drosophila pseudoobscura. Heterosis did not appear to be so evident under optimal environmental conditions, but was manifested more readily under stringent conditions where temperature, oxygen, food supply, or some other factor became limiting. Genotypic-environmental interactions in Drosophila melanogaster, as reported by Parsons (28) indicate that the F_1 hybrids were less variable than inbred lines for hatchability of eggs and emergence of larvae in adults. The inbred lines were characterized by a large genotype-environmental interaction and thus had a poorer homeostatic mechanism than the hybrids.

Thoday (37) studied the relationships between homeostasis and heterozygosity in artifically selected populations. He presents and supports the two hypotheses that: (1) artificial selection must produce deterioration of developmental homeostasis, and (2) that the deterioration must be the result of decreased heterozygosity. If

inbreeding is involved in artificial selection, heterozygosity and developmental homeostasis will be reduced to the point where natural selection for the heterozygote will balance artificial selection so that no further progress will be possible.

The hypothesis that buffered behavior of cross-fertilized organisms rests on a certain obligate level of heterozygosity was investigated by Lerner (21). He concluded that the phenotypic variability of genetically homogenous populations is an index of buffering capacity, since it measures the degree of departure of individual phenotypes from the average or norm of the group considered. Genotypes which endow the organism with better homeostatic properties may be referred to as buffered genotypes. This would be a relative thing since all genotypes have homeostatic properties in some degree.

Lewontin (24), in his studies of homeostasis and heterozygosity also pointed out that homeostasis is a relative term by which genotypes or groups of genotypes may be compared. It refers to the ability to adjust adaptively to varying environments and a direct measure of homeostasis is the mean adaptive value of a genotype over a determined set of environments. He studied the variance of abdominal bristle number of homozygotes, F_1's and F_2's of Drosophila melanogaster. The homozygotes, which are less homeostatic than heterozygotes constituted from them, show a lower variance in total bristle number than do the heterozygotes or F_2 populations. However, both the heterozygotes and F_2 populations show a higher correlation in bristle

number between the two segments examined. He suggests that there is no direct relation between phenotypic variance and homeostasis, but a higher phenotypic correlation between two parts of the same organism might be more often than not an indication of superior homeostatic adjustment.

The use of the term homeostasis by Lewontin (24) was questioned by Dempster (7), who referred back to Cannon's (3) original definition to point out that homeostasis is a condition that may vary but is relatively constant. He stated "It seems clear . . . that homeostasis applies to particular conditions that are maintained in a relatively stable state by special mechanisms that have evolved through natural selection; whereas the causative conditions, which are themselves variable, are called homeostatic devises or mechanisms. Homeostatic conditions seem important aids to, or components of, fitness, but not fitness itself."

In his reply to Dempster's comments, Lewontin (25) argued that the increase in average fitness and the increase in homeostatic adjustment are inter-related because all aspects of physiology and morphology of an organism are concerned with homeostatic adjustments.

Chai (4) investigated the possible changes in variability that may occur during the development of an organism. By comparing body weight and rate of growth of mice, he determined that differences in variability occurred during growth. In genetically

homogenous populations, the variability decreased as the animals matured, while in genetically heterogenous populations, the variability increased.

Tebb and Thoday (34) emphasize the danger of concluding that heterozygosity necessarily promotes homeostasis. They introduce the concept of "balance," or the co-ordination of the different physiological activities within the organism, to explain why some homozygotes can be superior to "unbalanced" heterozygotes. In further studies with Drosophila along this same line, Thoday (36) investigated the role of heterozygosity in the promotion of developmental flexibility. His results indicate that heterozygosity as such is not the essential cause of homeostasis.

The use of double-cross hybrids to overcome the problems of small seed size and poor seedling vigor in corn while still retaining hybrid vigor at its maximum was proposed by Jones (16). The double-cross population is a composite of hybrids that differ in their genetic constitution but individually they are all first generation hybrids. An additional advantage, lying in their genetic variability, is that they may be more adaptable to different seasonal conditions because all the plants will not be developing at the same time. Also, a proportion of the genotypes may be well-adapted to various conditions, giving a homeostatic type stability to the population. A single-cross population might be uniformly adversely affected by its environment.

Jones (17) compared the variability in corn of single-crosses (F_1), first generation double-crosses ($F_1 \times F_1$) and second generation double-crosses (F_2). He noted that the $F_1 \times F_1$ plants were noticeably different from the F_2 plants in the field and that they were characterized by even size, similar appearance, and general excellence. In characters which are greatly influenced by the plant's vigor (height, ear length, yield), the average $F_1 \times F_1$ was less variable than the average F_2. He states that "the $F_1 \times F_1$ plants are uniformly vigorous and are not dependent upon exceptional individuals for their high average position." No comparisons were discussed using the F_1 parents average variability because they were grown in a different year. He felt valid conclusions could not be made.

The importance of homeostasis in hybrid corn was illustrated by Jones (19) in his comparison of the variability of yield of two series of single- and double-crosses. Although the highest yields were usually obtained from a single-cross, they were more erratic in performance from location-to-location and from year-to-year. While the double-crosses were more variable in their genetic composition, they were more stable and more consistent in their performance. The average yield of the two groups was not significantly different and both had high levels of heterozygosity and heterosis.

Significantly higher yields were found in single-crosses and three-way crosses over double-crosses of maize by Stringfield (33).

The data indicate that the expression of hybrid vigor as a function of added and equal proportions of heterozygosis is arithmetic rather than geometric. This could explain the slight, but significantly greater vigor found in single- and three-way crosses when compared with double-crosses.

A comparison of various components in corn yield trials by Sprague and Federer (31) showed that the average value of single-crosses is more affected by variations in environment than either double- or top-crosses. These interactions were more important when the environments were most extreme as evidenced by greater year-hybrid interactions relative to location-hybrid interactions. The data suggest that the narrow genetic base characteristic of single-crosses makes for greater variation in yield response from year-to-year as well as from location-to-location.

Gamble (11) obtained essentially the same results using six inbred lines, and all possible F_1 crosses, F_2's, and backcrosses of corn. The crosses interacted more with years than with locations for the gene effects of all six attributes considered (yield, height, kernel row number, ear length, ear diameter, kernel weight). The location-cross interactions were relatively low and may be underestimated because the two locations were only 20 miles apart. He stresses the importance of conducting tests over a number of years rather than several tests at different locations in one year, but that duration of the evaluation tests may be shortened by conducting the

tests at more locations having very different environments over fewer years.

The implications of genetic variances in a hybrid breeding program were studied by Cockerham (5). Double-crosses not only produce seed more economically, but also dampen the effects of genotype-environment interactions because of the mixture of genotypes. He proposes that the use of somewhat related lines in each of the parental single-crosses will allow selection of double-crosses that approach the best single-cross. The general prevalence of genotype-environment interactions does not rule out the possibility that many specific genotypes may have wide adaptations.

Lewis (22) defines the term "phenotypic stability" as the ability to reach a norm of phenotypic expression in a wide range of environments. The testing of this character may require several different locations. His studies of pure lines of tomatoes indicated differences in phenotypic stability among the lines. The F_1 hybrid was much more stable than either of the parents, while stability in the F_3 generation ranged from that of the highly stable F_1 to that of the least stable parent. In this species, phenotypic stability is apparently under genetic control and therefore will respond to selection.

Mather (26) investigated stability in development by studying asymmetry, and its variation, in bilateral structures which show little or no difference between the average expressions of the two

sides of individual Drosophila. The differences between the sides (variance) was greatest in the inbred lines, and the least in the F_2's. The differences between the groups were not significant but the combined F_1's and F_2's were significantly different from the inbred parents.

An investigation of the effects of heterozygosity in inbreeding species was conducted by Jinks and Mather (15) using Nicotiana rustica. Heterozygosity itself, conferred no greater stability of development to the F_1's as compared with the parental lines. Stability in development reflects a genic balance produced by the action of natural selection. Paxman (29), using the same species, obtained the same results. A comparison of the stability of floral characteristics of different varieties indicated that variation was present between varieties in respect to stability. The inbred parents as a whole did not differ from the mean F_1. The within-plant variations of floral parts showed a common stability of floral parts while leaf stability was found to be independent. There was some evidence that control was not general throughout the plant.

The use of transformations to stabilize variances was discussed by Federer, Powers, and Payne (10) in their studies of chemical genetic data using sugar beets. In their data, there was a positive relationship between the mean and the total variance and they used a logarithmetic transformation to remove this dependency of mean on variance. They point out, however, that a variance stabilizing

transformation is not always desirable, and may even be impossible, if some of the populations sampled are genetically more variable than others.

MATERIALS AND METHODS

Plant Material

This study was conducted over the three year period, 1960-62. Test materials the first year included six double-crosses and their ten parental single-crosses. Test materials the second and third years included a different group of hybrids.

The material used in 1960 included six South Dakota hybrids and ten single-crosses that are all more or less adapted to this area, namely:

Double-cross entries	Single-cross entries	
SD 210 (SD5r x B8) (SD26 x A509)	(Oh56A x B8)	(SD5r x B8)
SD 220 (SD26 x B8) (SD5 x SD48)	(M14 x SD5)	(SD26 x A509)
SD 250 (Oh56A x B8) (M14 x SD5)	(Oh56A x SD7)	(Wf_9 x M14)
SD 262 (Oh56A x SD6) (M14 x SD5)	(Oh56A x SD6)	(SD5 x SD7)
SD 270 (Oh56A x SD7) (M14 x SD5)	(SD26 x B8)	
SD 400 (Wf_9 x M14) (SD5 x SD7)	(SD5 x SD48)	

The double-cross seed was obtained from Sokota Hybrid Producers, Brookings, and the single-cross seed was obtained from the Foundation Seed Stock Division of the South Dakota State College Foundation.

The material used in 1961 and 1962 included fifteen single-crosses, and three double-crosses as presented in Table I. The entry designations indicated (SC-1, SC-2, etc.) will be used in subsequent tables and discussion.

Table I. Entry Designations for 1961-62 Plant Materials

Single-crosses

SC-1	(SD5 x I153RM)	SC-9	(I153RM x M14)
SC-2	(SD5 x B8)	SC-10	(B8 X Oh43)
SC-3	(SD5 x Oh43)	SC-11	(B8 x Oh56A)
SC-4	(SD5 x Oh56A)	SC-12	(B8 x M14)
SC-5	(SD5 x M14)	SC-13	(Oh43 x Oh56A)
SC-6	(I153RM x B8)	SC-14	(Oh43 x M14)
SC-7	(I153RM x Oh43)	SC-15	(Oh56A x M14)
SC-8	(I153RM x Oh56A)		

Double-crosses

DC-1	(Oh56A x B8) (M14 x SD5)
DC-2	(Oh56A x B8) (I153RM x Oh43)
DC-3	(M14 x SD5) (I153RM x Oh43)

Inbred seed required to produce the single-crosses and single-cross seed needed to produce the double-crosses was obtained from sources maintained by the Agronomy Department, South Dakota State College. These were planted in the corn nursery in 1960 and 1961, and the necessary crosses were made each year to obtain sufficient seed for the following year's tests.

Plot Location

The tests were conducted in six locations (see Table II) in each of the three years. Five of the plots were in Brookings County and one in Moody County. The locations were selected on the basis of soil type as determined from soil survey maps.

Table II. Plot Locations and Soil Type.

Location	Soil Type
15 mi SW of Brookings	Flandreau loam
2 mi N of Brookings	Vienna loam
8 mi SE of Dell Rapids	Moody silty loam
5 mi SW of Brookings	Fordville loam
8 mi NW of Brookings	Hecla sandy loam
25 mi NE of Brookings	Singsaas loam

These soil differences, along with variations in climate from location-to-location and year-to-year, would provide as wide a range as possible of environmental conditions in this area. A wide range would be desirable in order to detect differences in the homeostatic properties of the entries.

The plots were located in co-operating farmers' fields and had a minimum of two border rows on the outside edges. Weed control was accomplished by the farmer and only large competitive weeds such as sunflower and cocklebur were removed by hand. No fertilizer, other than what the farmer may have used, was applied to any of the plots. One location (Fordville loam) was on the Agricultural Engineering Farm where it was sprinkler-irrigated.

Climatological Data

The climate was generally quite favorable for corn growth during the years 1960-62. Some minor variations were noted from location-to-location and from year-to-year. Climatic information

was obtained from the annual reports published by the United States Department of Commerce, Office of State Climatologist, of data obtained at Brookings. Brookings is more-or-less the geographical center of the plot locations. No climatological data were recorded at any of the locations.

The 1960 growing season was characterized by a slightly cool June (1.77°F below average) but the rest of the season was about average. Precipitation also was about average for the entire growing season, although it was 1.77 inches below average in July and 2.86 inches above average in August.

A relatively cool season prevailed in 1961, with the temperature being 3.5 to 4.0°F below average throughout the entire growing season. Precipitation that was 2.0 inches above normal in May delayed planting in some locations. Rainfall was only slightly below normal during the remainder of the season.

Nineteen sixty two had an abundance of moisture during the early part of the season, with precipitation averaging 8.5 inches above normal for the period May through July. Some departure from normal was observed for temperatures. May was relatively warm, being 2.5°F above average, and July was cool, with temperatures averaging 4.7°F below average.

These variations were not extreme enough in any one year, or any one location to drastically affect the growth and development of the plant materials.

Field Plot Design and Data Recorded

The design each year was a randomized complete block, with four replications (blocks), so that each entry occurred once in each block. The seed was treated and hand planted in rows that the co-operating farmers had marked.

Each entry in each replication consisted of three rows, forty inches apart and fifty feet long. The plants were spaced approximately fourteen inches apart in the rows. The middle row of each entry was planted to two kernels per hill with the stand being thinned about two weeks after emergence to one plant each fourteen inches. Missing hills were replanted with a purple marker line to provide competition.

Measurements were taken on the first twenty plants in each center row that had equal competition on all four sides. Plant heights were measured from ground level to the base of the flag (uppermost) leaf. Measurements were made about the first of August when growth was assumed to have ceased. Ears were harvested from twenty plants in each row about the first of October, individually bagged, and dried for approximately two months at 100°F before being weighed.

The sampled plants were not individually marked at the time height measurements were taken, but the first and twentieth sampled plants in each row were tagged. In some cases, these tags had fallen off by harvest time, so it is possible that plant height and ear weight data were not always obtained from the same twenty plants.

Perfect stands were not obtained in all cases, resulting in less than twenty harvestable plants per replication. With one exception, these losses were not considered large enough to have any bearing on the statistical analyses. The 1961 plot on the Hecla sandy loam had such a poor stand that the entire plot was abandoned and no data were recorded.

Statistical Analyses

Plot means and variances were calculated and an analysis of variance was made on each year's data. A comparison of the means and variances suggested that a relationship existed and that the variance was not homogeneous between entries. A portion of the 1960 data was tested by use of "Bartlett's" test of homogeneity of variance and the results are presented in Table III. These results indicate that differences in variance were present in at least some of the entry classes.

A logarithmetic transformation seemed suitable for removing the dependency of means on variances and a portion of the data was so transformed. Subsequent retesting by use of "Bartlett's" test indicated that the transformation was not satisfactory in all cases. As an example, the X^2 value of 49.140 for the single-cross class at the Singsaas location was raised to 183.398** after logarithmetic transformation. Analysis of ear weight means and variances gave similar results.

Table III. Values of X^2 For 1960 Plant Height Variance.

Class	d.f.	Vienna	Fordville	Singsaas
Double-cross	5	18.236**	8.943	14.928**
Single-cross	9	19.559*	9.031	49.140*

d.f. degrees of freedom
** Significant at 1% level
* Significant at 5% level

Re-evaluation of the problem at this point indicated that a satisfactory transformation had not been found. It was assumed that some entries, or some classes of entries, were genetically more variable than others. Any transformation that stabilized the variance would prevent the detection of differences in variability between the classes.

The analysis used consisted of comparison of the grand means by use of Duncan's new multiple range test (14) at the 5% level. The replications-in-locations source of variation provided the error mean square used in calculating the significant ranges. Justification for use of this method is presented in the discussion.

Variances of the entries were pooled over locations, and where possible, over years. Comparisons were made by computation of confidence intervals for the variance estimates. Since the degrees of freedom for chi-square exceeded those listed in tables commonly used, values were calculated using the formula presented by Hald (12).

The formula is: $X_p^2 = \frac{1}{2}(\sqrt{2f-1} \pm \mu p)^2$, where p is the probability level under the normal curve and f is the degrees of freedom. A value of 1.96 for μ was used for testing at 97½% level or the 2½% level depending on the sign preceeding μ. The non-symmetrical distribution of X^2 necessitated calculation of upper and lower points to obtain the confidence interval.

EXPERIMENTAL RESULTS

Table IV presents the plant height and Table V the ear weight means for each entry in each of the six locations in 1960. As expected, in all locations, a single-cross had the greatest mean height, and with one exception, it was a different single-cross in each location. The ear weight means show one double-cross (SD 270) excelling in two locations and one single-cross (Wf_9 x M14) in the other four locations.

A comparison of the 1960 grand means is presented in Table VI. Only minor significant differences were found for both plant height and ear weight mean values averaged over all locations.

Tables VII and VIII show the plant height and ear weight means, respectively, for the 1961 and 1962 data. The same entries were used both years, so the data were combined and treated as eleven locations, (five in 1961 and six in 1962). No comparisons were made for differences between years as such. It may be noted in Table VII that one single-cross (SC-10) had the highest mean height in six locations, all of which were in 1962. Another single-cross (SC-12) had the highest mean height in four locations, with a double-cross highest in the remaining location.

The ear weight means in Table VIII do not show any one entry being as consistent in highest value. SD-10 excelled in three locations, SC-12 and SC-15 in two each and SC-1, SC-9, and SC-13 in one location. A double-cross (DC-2) was highest in one location.

Table IV. 1960 Plant Height Means (Inches)

Entry	Location						Grand Mean
	1	2	3	4	5	6	
(Oh56A x B8)	51.6	54.1	65.3	72.3	51.5	61.1	59.3
(M14 x SD5)	52.5	50.6	58.9	64.3	50.0	55.0	55.2
(Oh56A x SD7)	53.0	52.9	64.8	71.4	45.8	60.9	58.1
(Oh56A x SD6)	50.3	52.9	60.2	65.4	50.4	52.9	55.4
(SD26 x B8)	49.2	56.6	64.8	67.6	55.8	57.8	58.6
(SD5 x SD48)	49.5	42.6	47.3	50.6	42.5	43.2	50.0
(SD5r x B8)	50.6	54.0	61.3	64.6	54.0	55.6	56.7
(SD26 x A509)	51.4	52.3	57.2	58.9	52.1	52.2	54.0
(Wf_9 x M14)	49.8	52.8	63.8	78.8	48.5	60.0	59.0
(SD5 x SD7)	51.9	54.5	60.0	66.2	46.7	56.0	55.9
SD 210	49.2	52.6	59.6	64.6	50.4	54.0	55.1
SD 220	50.8	53.0	58.5	62.2	53.0	54.0	55.2
SD 250	52.3	53.4	61.5	69.9	45.1	60.0	57.0
SD 262	50.2	52.8	58.4	66.8	49.8	56.8	55.8
SD 270	52.0	53.6	63.5	71.1	48.5	60.4	58.2
SD 400	52.4	54.0	61.6	72.0	49.2	59.1	58.0

Table V. 1960 Ear Weight Means (Grams)

Entry	Location						Grand Mean
	1	2	3	4	5	6	
(Oh56A x B8)	176.6	203.3	155.2	232.4	197.4	191.4	192.7
(M14 x SD5)	176.2	193.6	129.0	217.8	150.8	172.0	173.2
(Oh56A x SD7)	172.3	222.3	157.0	215.7	161.6	195.5	187.4
(Oh56A x SD6)	179.2	223.8	163.2	198.3	167.5	191.6	187.3
(SD26 x B8)	158.1	175.6	158.9	189.7	157.1	170.6	168.3
(SD5 x SD48)	149.6	125.9	115.6	115.5	95.1	131.8	122.2
(SD5r x B8)	160.3	167.7	149.8	192.8	146.7	160.8	163.0
(SD26 x A509)	171.4	172.6	156.2	172.8	157.9	168.7	166.6
(Wf_9 x M14)	172.4	232.4	166.0	253.1	204.0	213.7	206.9
(SD 5 x SD7)	170.9	187.2	142.4	193.1	124.4	179.4	166.2
SD 210	164.6	199.9	156.0	211.2	130.3	186.9	174.8
SD 220	172.9	169.2	149.9	183.2	155.8	165.7	166.1
SD 250	164.6	199.6	156.0	211.2	130.3	186.9	174.8
SD 262	165.8	191.5	151.3	210.7	174.6	180.4	179.0
SD 270	189.4	212.5	177.4	203.4	165.4	196.4	190.8
SD 400	165.8	206.7	172.5	228.0	162.8	189.2	187.5

Table VI. Comparison of 1960 Plant Height and Ear Weight Means (Duncan's Multiple Range Test at 5% level)

Plant Height		Ear Weight	
Entry	Mean	Entry	Mean
(Oh56A x B8)	59.3	(Wf_9 x M14)	206.9
(Wf_9 x M14)	59.0	(Oh56A x B8)	192.7
(SD26 x B8)	58.6	SD 270	190.8
SD 270	58.2	SD 400	187.5
(Oh56A x SD7)	58.1	(Oh56A x SD7)	187.4
SD 400	58.0	(Oh56A x SD5)	187.3
SD 250	57.0	SD 262	179.0
(SD5r x B8)	56.7	SD 250	174.8
(SD5 x SD7)	55.9	SD 210	174.8
SD 262	55.8	(M14 x SD5)	173.2
(Oh56A x SD6)	55.4	(SD26 x B8)	168.3
(M14 x SD5)	55.2	(SD26 x A509)	166.6
SD 220	55.2	(SD5 x SD7)	166.2
SD 210	55.1	SD 220	166.1
(SD26 x A509)	54.0	(SD5r x B8)	163.0
(SD5 x SD48)	50.0	(SD5 x SD48)	122.2

Table IX shows the extremely wide ranges of significant differences for grand mean values of plant height. The ear weight means varied less and fewer differences were found.

Comparisons of the means was of interest but the problem was more concerned with single- vs double-cross variability between and within locations. Tables X through XIII present the total, between-location, and within-location sums of squares for plant height and ear weight as computed from the 1960 and the combined 1961-62 data. Confidence limits for the variance estimates were computed and are graphically presented in Figures 1 through 8.

Table VII. 1961 and 1962 Plant Height Means (Inches)

Entry	Location 1961					Location 1962						Grand Means
	1	2	3	4	6	1	2	3	4	5	6	
SC-1	59.0	59.3	64.7	62.5	61.5	64.4	65.5	57.6	63.5	59.3	60.9	61.6
SC-2	62.2	66.7	67.4	66.3	66.1	66.6	71.3	62.5	65.4	60.8	65.3	65.5
SC-3	57.8	61.7	65.6	67.8	64.1	67.5	67.8	59.6	66.5	63.4	63.8	64.1
SC-4	61.7	66.7	68.4	66.4	66.9	67.2	66.0	63.2	65.0	61.6	64.3	65.2
SC-5	62.5	67.0	67.8	66.8	64.7	64.2	70.3	61.8	65.2	64.1	64.2	65.3
SC-6	71.0	79.8	78.8	77.9	74.2	75.6	79.0	70.2	72.3	70.5	72.3	74.7
SC-7	65.9	71.9	71.5	68.6	75.8	72.6	72.3	66.7	68.4	68.1	69.2	70.1
SC-8	66.4	72.0	69.9	67.0	69.1	69.0	64.5	67.1	61.1	61.6	64.9	66.6
SC-9	70.8	79.3	73.8	74.0	71.7	67.7	70.5	67.2	67.5	64.8	66.4	70.3
SC-10	69.9	77.4	76.6	73.7	77.5	81.1	81.1	78.7	80.0	74.3	73.5	76.7
SC-11	70.1	79.1	77.1	77.3	76.1	75.0	74.6	69.8	69.0	67.4	70.7	73.3
SC-12	73.8	80.9	80.1	77.9	74.0	70.9	77.9	72.3	70.8	70.5	71.9	74.6
SC-13	71.0	77.5	77.5	77.7	76.1	75.4	77.2	69.5	76.3	70.3	70.4	74.4
SC-14	70.2	74.0	73.7	73.3	71.5	69.5	74.7	70.6	72.4	71.4	68.2	71.8
SC-15	68.1	77.0	78.0	71.5	72.7	65.3	70.4	66.8	66.5	64.8	66.0	69.7
DC-1	67.3	72.0	71.0	73.1	70.3	73.7	72.6	66.4	68.1	67.2	66.6	69.8
DC-2	70.5	77.7	73.8	74.0	79.1	77.6	75.4	70.6	74.3	69.4	70.8	73.9
DC-3	64.6	67.4	68.2	67.3	67.7	73.7	73.0	67.5	69.6	67.8	66.7	68.5

Table VIII. 1961 and 1962 Ear Weight Means (Grams)

	Location											Grand Mean
	1961					1962						
	1	2	3	4	6	1	2	3	4	5	6	
SC-1	136.8	153.2	186.0	190.4	175.2	181.7	182.4	162.5	182.5	194.1	174.9	174.5
SC-2	140.4	167.6	170.9	191.0	175.6	172.9	162.5	166.2	171.4	177.0	168.9	169.5
SC-3	145.7	165.1	176.9	217.2	186.0	178.8	177.6	177.9	185.4	188.1	181.0	180.0
SC-4	134.8	162.1	161.5	199.4	192.2	178.4	166.7	176.6	161.4	189.8	174.0	172.4
SC-5	139.8	159.8	178.9	199.0	185.8	191.9	174.7	160.0	196.6	191.8	181.8	178.2
SC-6	146.3	201.4	174.8	224.4	209.8	196.6	185.4	174.5	179.7	203.7	207.5	191.3
SC-7	139.8	157.5	181.9	209.3	192.4	180.9	184.8	172.4	175.9	187.3	177.5	178.2
SC-8	144.3	177.0	160.9	228.6	200.9	214.5	197.7	186.4	209.8	223.9	202.6	195.1
SC-9	147.4	164.9	153.3	215.1	198.4	209.0	201.9	280.4	206.1	225.6	196.6	199.9
SC-10	184.9	174.7	175.0	237.7	191.4	211.5	203.6	181.5	224.8	214.9	272.5	206.6
SC-11	133.3	164.6	159.7	222.5	215.0	177.9	190.8	178.4	199.5	183.2	173.1	181.6
SC-12	250.5	260.4	180.8	223.1	181.8	198.6	187.7	180.8	187.7	208.4	183.0	203.9
SC-13	146.3	151.2	182.0	213.2	195.0	194.4	204.1	162.2	211.8	293.3	183.8	194.3
SC-14	163.2	160.2	182.1	224.5	184.2	204.8	194.5	184.9	214.4	209.6	181.3	191.2
SC-15	129.2	152.0	165.6	207.6	190.0	218.6	213.6	257.5	224.7	200.6	178.9	194.4
DC-1	145.4	159.8	149.2	212.0	204.8	210.3	198.5	168.2	178.0	191.0	180.2	181.6
DC-2	139.4	164.9	169.2	216.6	219.9	202.4	190.8	181.5	188.3	219.4	200.7	190.3
DC-3	153.5	171.0	154.1	218.4	198.4	210.1	200.4	173.6	191.1	206.0	174.1	186.4

Table IX. Comparison of 1961-1962 Plant Height and Ear Weight Means (Duncan's Multiple Range Test at 5% level).

Plant Height		Ear Weight	
Entry	Mean	Entry	Mean
SC-10	76.7	SC-10	206.6
SC-6	74.7	SC-12	203.9
SC-12	74.6	SC-9	199.9
SC-13	74.4	SC-8	195.1
DC-2	73.9	SC-15	194.4
SC-11	73.3	SC-13	194.3
SC-14	71.8	SC-6	191.3
SC-9	70.3	SC-14	191.2
SC-7	70.1	DC-2	190.3
DC-1	69.8	DC-3	186.4
SC-15	69.7	DC-1	181.6
DC-3	68.5	SC-11	181.6
SC-8	66.6	SC-3	180.0
SC-2	65.5	SC-5	178.2
SC-5	65.3	SC-7	178.2
SC-4	65.2	SC-1	174.5
SC-3	64.1	SC-4	172.4
SC-1	61.6	SC-2	169.5

The data from Table X as illustrated in Figure 1, show an overlapping of the confidence intervals. This indicates there were no clear-cut differences in the between-location variability for plant height of the single-cross and double-cross classes. Figure 2 gives an indication of a slightly lower within-location variability for the single-crosses. There are several exceptions, but as a whole, the single-crosses as a group tended to be less variable than the double-crosses as a group. 1960 ear weight variability data (Table XI) shows no trends as to differences between-locations

Table X. 1960 Plant Height Sums of Squares and Confidence Intervals for Variance Estimates (5% Level)

Entry	Total Sum of Squares	Between Locations			Within Locations		
		Sum of Squares	d.f.	Confidence Interval	Sum of Squares	d.f.	Confidence Interval
(Oh56A X B8)	39,083	27,669	5	2,162 to 33,296	11,414	455	42.2 to 61.0
(M14 X SD5)	23,229	12,583	5	983 to 15,141	10,646	449	39.8 to 57.7
(Oh56A X SD7)	42,881	33,384	5	2,608 to 40,173	9,497	474	33.8 to 48.1
(Oh56A X SD6)	22,652	13,613	5	1,089 to 16,382	9,039	466	32.7 to 47.0
(SD26 X B8)	24,929	15,066	5	1,179 to 18,129	9,863	474	35.1 to 50.4
(SD5 X SD48)	15,343	4,256	5	332 to 5,122	11,087	474	39.4 to 56.6
(SD5r X B8)	20,274	11,538	5	901 to 13,884	8,736	466	31.6 to 45.5
(SD26 X A509)	12,149	4,010	5	3,133 to 48,253	8,139	469	29.2 to 42.1
(Wf9 X M14)	53,926	37,645	5	2,941 to 45,300	16,281	471	58.3 to 83.7
(SD5 X SD7)	75,923	16,769	5	1,310 to 20,179	59,154	474	210.5 to 302.1
SD 210	30,162	14,062	5	1,098 to 16,921	16,100	473	57.4 to 82.4
SD 220	15,264	6,154	5	481 to 7,405	9,110	474	32.4 to 46.5
SD 250	45,071	26,281	5	2,053 to 31,626	18,790	473	67.0 to 96.2
SD 262	31,032	16,220	5	1,267 to 19,519	14,812	474	52.7 to 75.7
SD 270	42,802	26,819	5	2,095 to 32,274	15,983	469	57.4 to 82.6
SD 400	42,723	26,431	5	2,065 to 31,807	16,292	474	83.2 to 58.0

d.f. = degrees of freedom

Figure 1. 1960 Plant Height Between-Locations Confidence Intervals for Variance Estimates (5% Level).

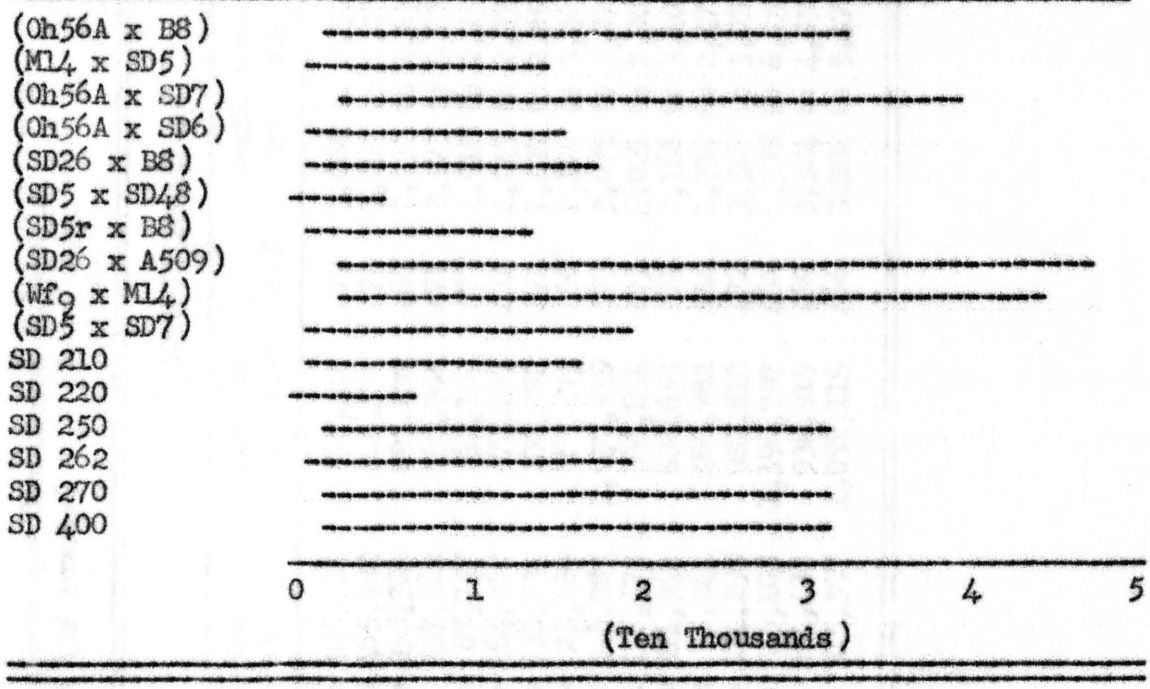


Figure 2. 1960 Plant Height Within-Locations Confidence Intervals for Variance Estimates (5% Level).

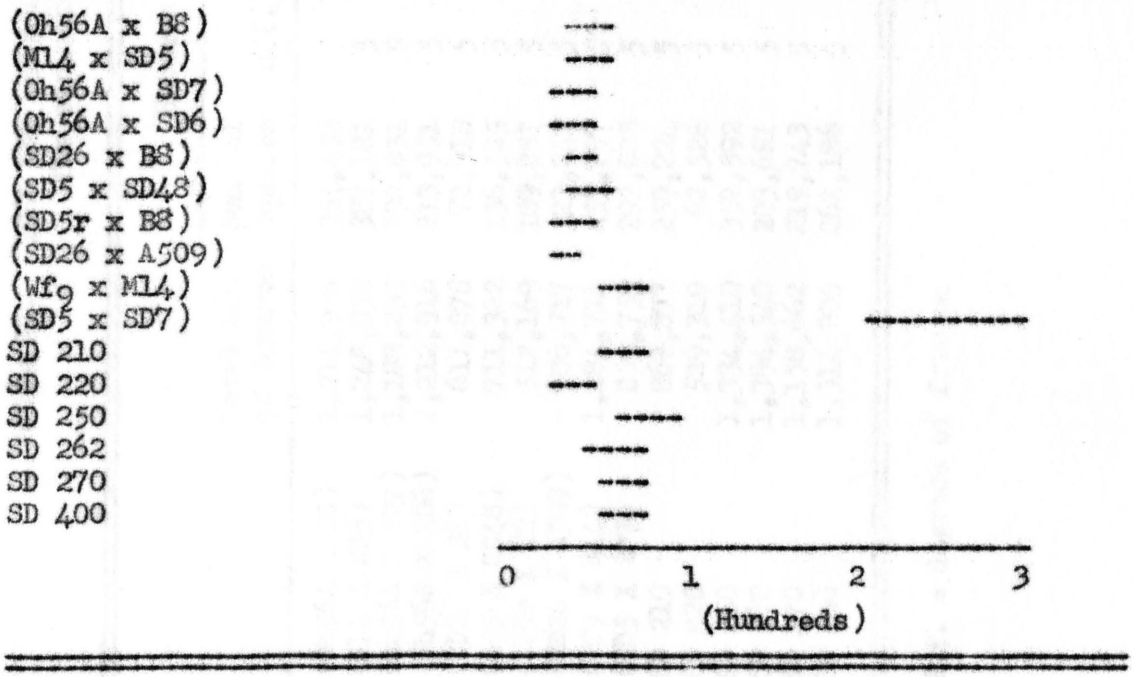


Table XI. 1960 Ear Weight Sums of Squares and Confidence Intervals for variance estimates (5% levels)

	Total Sum of Squares	Between Locations			Within Locations		
		Sum of Squares	d.f.	Confidence Interval	Sum of Squares	d.f.	Confidence Interval
(Oh56A X B8)	1,214,978	354,433	5	27,690 to 426,514	860,545	473	3,068 to 4,404
(M14 X SD5)	1,248,039	387,181	5	30,248 to 465,922	860,858	473	3,069 to 4,406
(Oh56A X SD7)	1,188,233	292,831	5	22,877 to 352,384	895,402	467	3,230 to 4,658
(Oh56A X SD6)	1,212,916	213,951	5	16,715 to 257,462	998,965	471	3,575 to 5,138
(SD26 X B8)	611,078	72,918	5	5,697 to 87,747	538,160	473	1,918 to 2,754
(SD5 X SD48)	711,322	136,525	5	10,666 to 164,290	574,797	474	2,045 to 2,936
(SD5r X B8)	512,169	109,887	5	8,585 to 132,235	402,282	474	1,431 to 2,055
(SD26 X A509)	606,717	23,242	5	1,816 to 27,969	583,475	462	2,126 to 3,065
(Wf9 X M14)	1,484,716	453,797	5	35,453 to 546,085	1,030,919	473	3,675 to 5,276
(SD5 X SD7)	859,759	292,905	5	22,883 to 352,473	566,854	473	2,021 to 2,901
SD 210	867,877	259,224	5	20,251 to 311,942	608,653	474	2,166 to 3,109
SD 220	529,310	62,528	5	4,885 to 75,244	466,782	458	1,714 to 2,479
SD 250	1,334,410	352,592	5	27,546 to 424,298	981,818	472	3,507 to 5,038
SD 262	1,394,540	203,681	5	15,912 to 245,103	1,190,797	462	4,338 to 6,256
SD 270	1,158,662	219,743	5	17,167 to 264,432	938,919	469	3,374 to 4,852
SD 400	1,314,305	262,186	5	20,483 to 315,507	1,052,119	466	3,802 to 5,475

d.f. = degrees of freedom

(Figure 3) or within-locations (Figure 4) between the single and double-cross groups although there was quite a range within the entire test.

The plant height variability for 1961-62 data (Table XII) show a slightly decreased variability for the double-cross data group between locations (Figure 5) as compared to the single-cross group. The within-locations variability (Figure 6) indicates a definite difference. With only one exception, the confidence intervals of the variance estimates of the single-crosses were lower and did not overlap the confidence intervals of the double-crosses.

Table XIII and Figures 7 and 8 indicate no general trends for ear weight in 1961-62 as to differences in the variability of the two groups, either between-locations or within-locations.

Figure 3. 1960 Ear Weight Between-Location Confidence Intervals for Variance Estimates (5% Level)

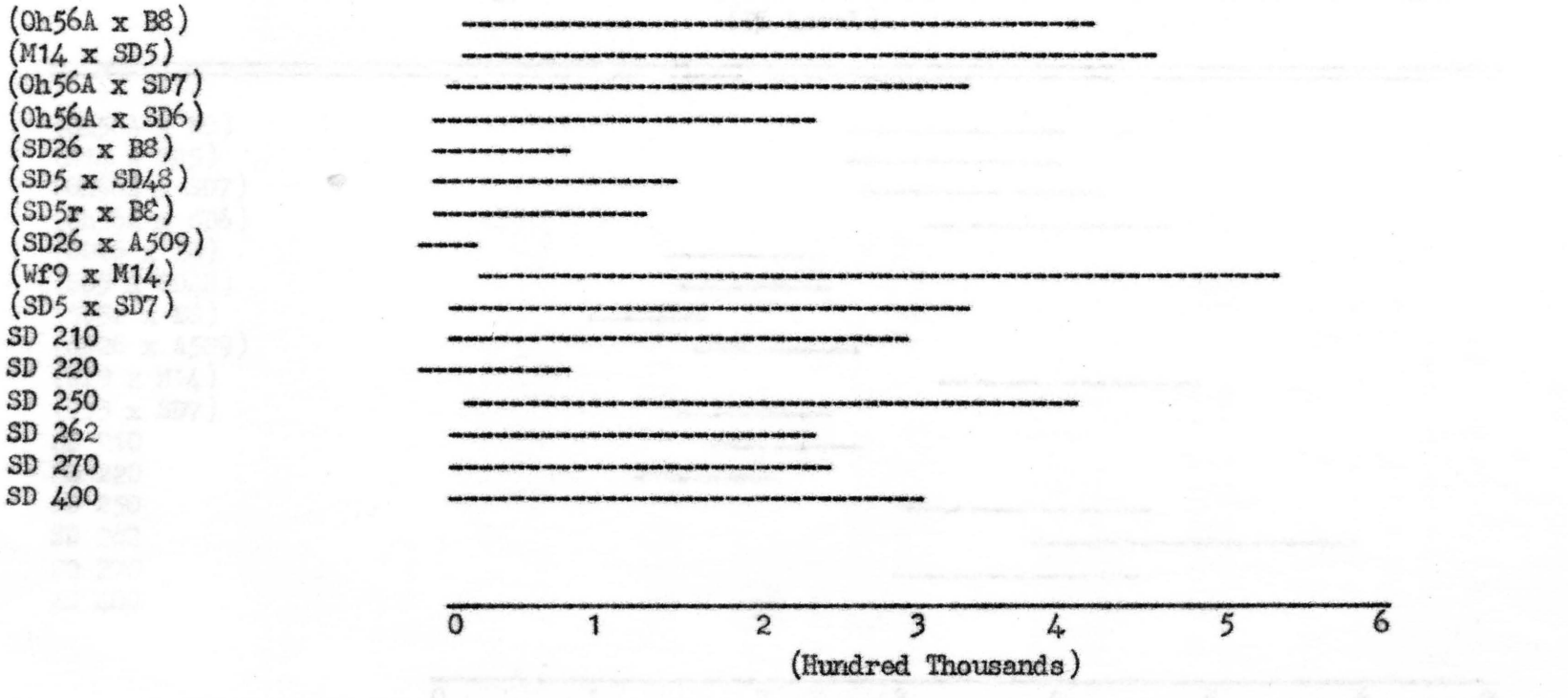


Figure 4. 1960 Ear Weight Within-Location Confidence Intervals for Variance Estimates (5% Level)

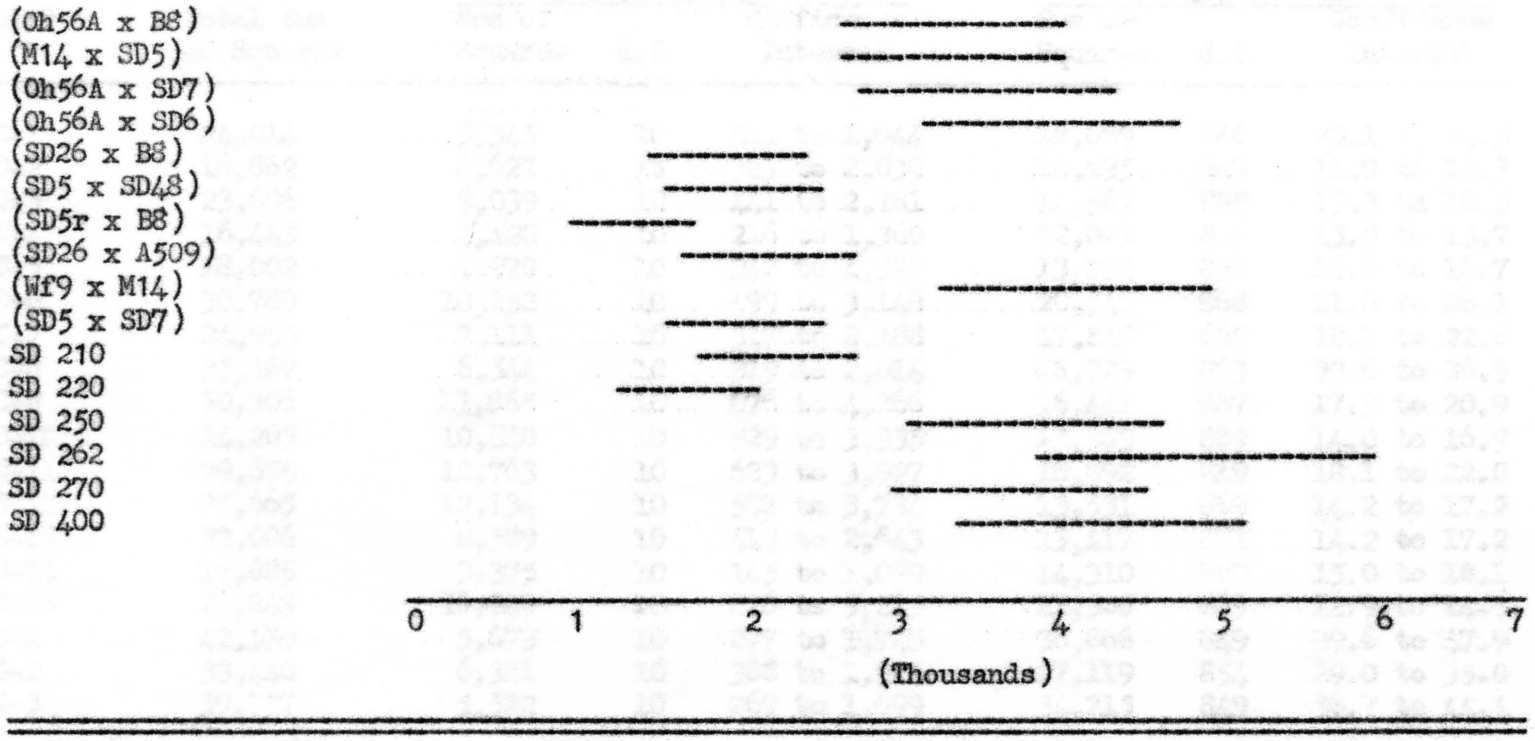


Table XII. 1961 and 1962 Plant Height Sums of Squares and Confidence Intervals for Variance Estimates (5% Level).

Entry	Total Sum of Squares	Between Locations			Within Locations		
		Sum of Squares	d.f.	Confidence Interval	Sum of Squares	d.f.	Confidence Interval
SC-1	24,014	5,345	10	261 to 1,644	18,669	846	20.1 to 24.3
SC-2	16,862	6,627	10	323 to 2,039	10,235	849	11.0 to 13.3
SC-3	23,606	9,039	10	441 to 2,781	14,567	869	15.3 to 18.5
SC-4	16,443	4,420	10	216 to 1,360	12,023	846	13.0 to 15.7
SC-5	18,002	4,970	10	242 to 1,529	13,032	858	13.8 to 16.7
SC-6	30,780	10,232	10	499 to 3,148	20,548	868	21.6 to 26.1
SC-7	24,955	7,111	10	347 to 2,188	17,843	869	18.7 to 22.6
SC-8	35,467	6,544	10	319 to 2,014	28,923	863	30.6 to 36.9
SC-9	30,306	13,865	10	676 to 4,266	16,441	867	17.3 to 20.9
SC-10	24,203	10,840	10	529 to 3,335	13,363	869	14.0 to 16.9
SC-11	29,655	12.763	10	623 to 3,927	16,892	849	18.1 to 22.0
SC-12	25,665	12,134	10	592 to 3,734	13,531	869	14.2 to 17.2
SC-13	22,006	8,589	10	419 to 2,643	13,417	861	14.2 to 17.2
SC-14	17,685	3,375	10	165 to 1,039	14,310	869	15.0 to 18.1
SC-15	28,249	16,949	10	826 to 5,215	11,300	869	11.9 to 14.3
DC-1	42,539	5,673	10	277 to 1,745	36,866	849	39.6 to 47.9
DC-2	33,440	6,321	10	308 to 1,945	27,119	854	29.0 to 35.0
DC-3	39,737	5,522	10	269 to 1,699	34,215	849	36.7 to 44.4

d.f. = degrees of freedom

Figure 5. 1961-62 Plant Height Between-Locations Confidence Intervals for Variance Estimates (5% Level).

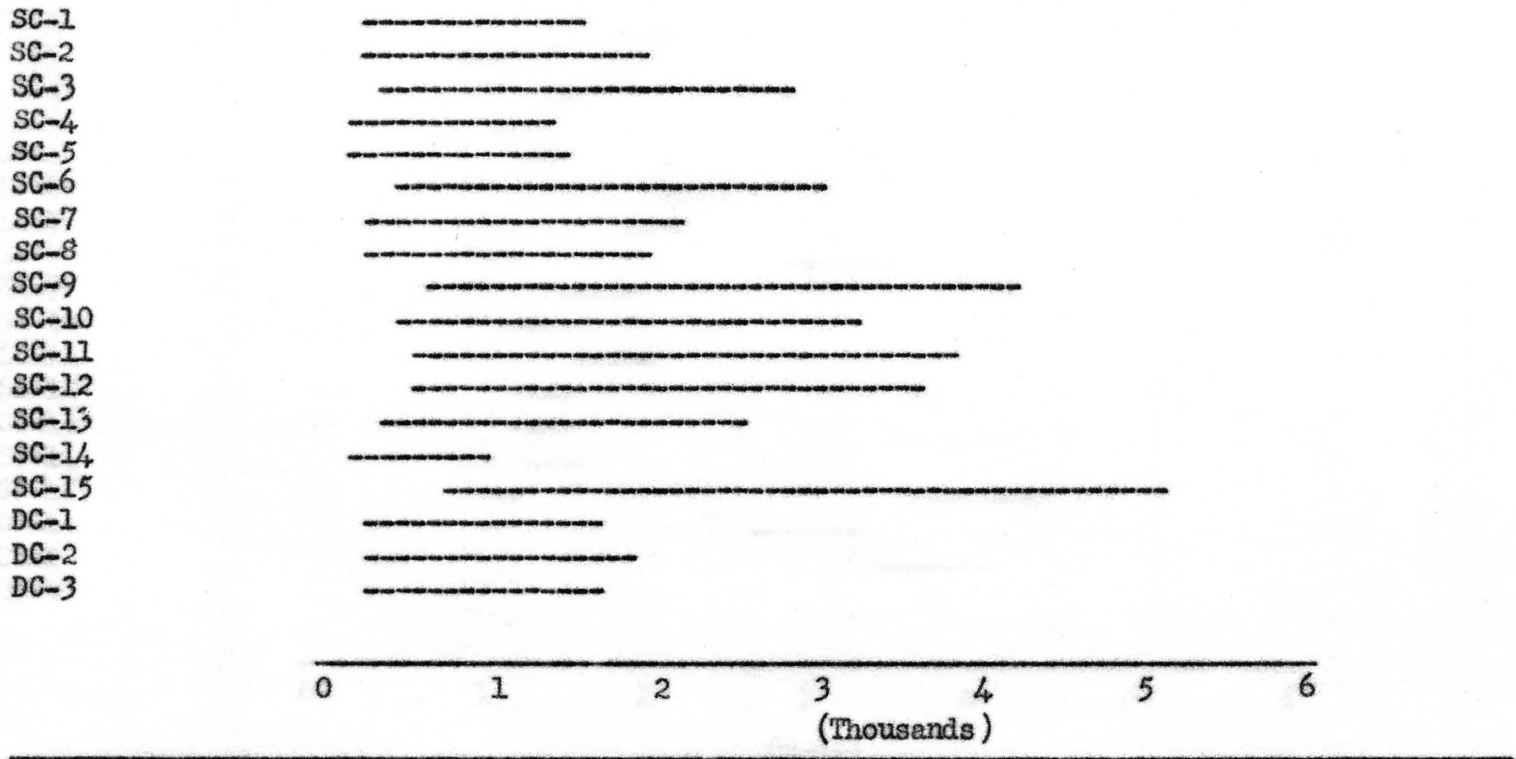


Figure 6. 1961-62 Plant Height Within-Locations Confidence Intervals for Variance Estimates (5% Level).

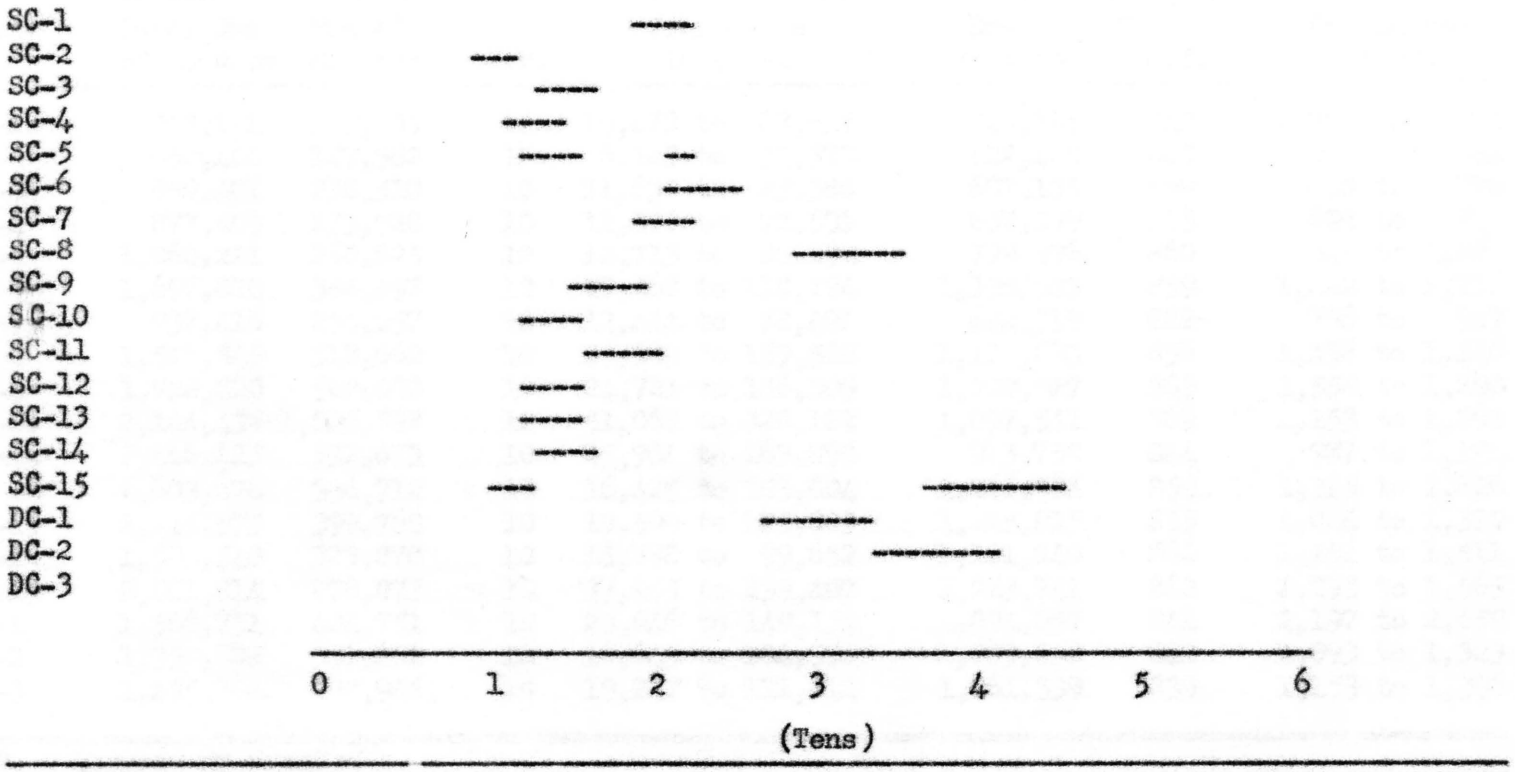


Table XIII. 1961 and 1962 Ear Weight Sums of Squares and Confidence Intervals for Variance Estimates (5% Levels)

Entry	Between Locations				Within Locations		
	Total Sum of Squares	Sum of Squares	d.f.	Confidence Interval	Sum of Squares	d.f.	Confidence Interval
SC-1	943,191	223,005	10	10,878 to 68,617	720,186	842	780 to 944
SC-2	650,400	127,982	10	6,243 to 39,379	522,418	843	565 to 684
SC-3	850,401	238,510	10	11,635 to 73,388	607,135	869	638 to 770
SC-4	873,409	235,920	10	11,508 to 72,591	637,489	835	695 to 843
SC-5	1,060,221	260,625	10	12,713 to 80,192	799,596	860	848 to 1,025
SC-6	1,697,020	358,097	10	17,468 to 110,184	1,338,923	859	1,422 to 1,718
SC-7	937,416	255,097	10	12,444 to 78,491	682,319	822	756 to 917
SC-8	1,541,545	518,662	10	25,300 to 159,588	1,122,833	856	1,196 to 1,446
SC-9	1,728,020	508,003	10	24,781 to 156,309	1,220,017	863	1,558 to 1,290
SC-10	2,144,438	1,046,897	10	51,068 to 322,122	1,097,541	869	1,153 to 1,392
SC-11	1,446,423	532,673	10	25,984 to 163,899	913,750	844	987 to 1,194
SC-12	1,603,676	336,712	10	16,425 to 103,604	1,266,964	859	1,345 to 1,626
SC-13	1,415,575	399,760	10	19,500 to 123,003	1,015,815	855	1,084 to 1,310
SC-14	1,505,710	323,870	10	15,798 to 99,652	1,181,840	862	1,251 to 1,511
SC-15	2,001,814	778,073	10	37,955 to 239,407	1,223,741	862	1,295 to 1,565
DC-1	1,566,751	484,751	10	23,646 to 149,154	2,034,057	844	2,197 to 2,659
DC-2	1,350,883	341,231	10	16,645 to 104,994	1,009,652	842	1,093 to 1,323
DC-3	1,455,284	393,945	10	19,217 to 121,214	1,061,339	839	1,153 to 1,396

d.f. = degrees of freedom

Figure 7. 1961-62 Ear Weight Between-Locations Confidence Intervals for Variance Estimates (5% Level).

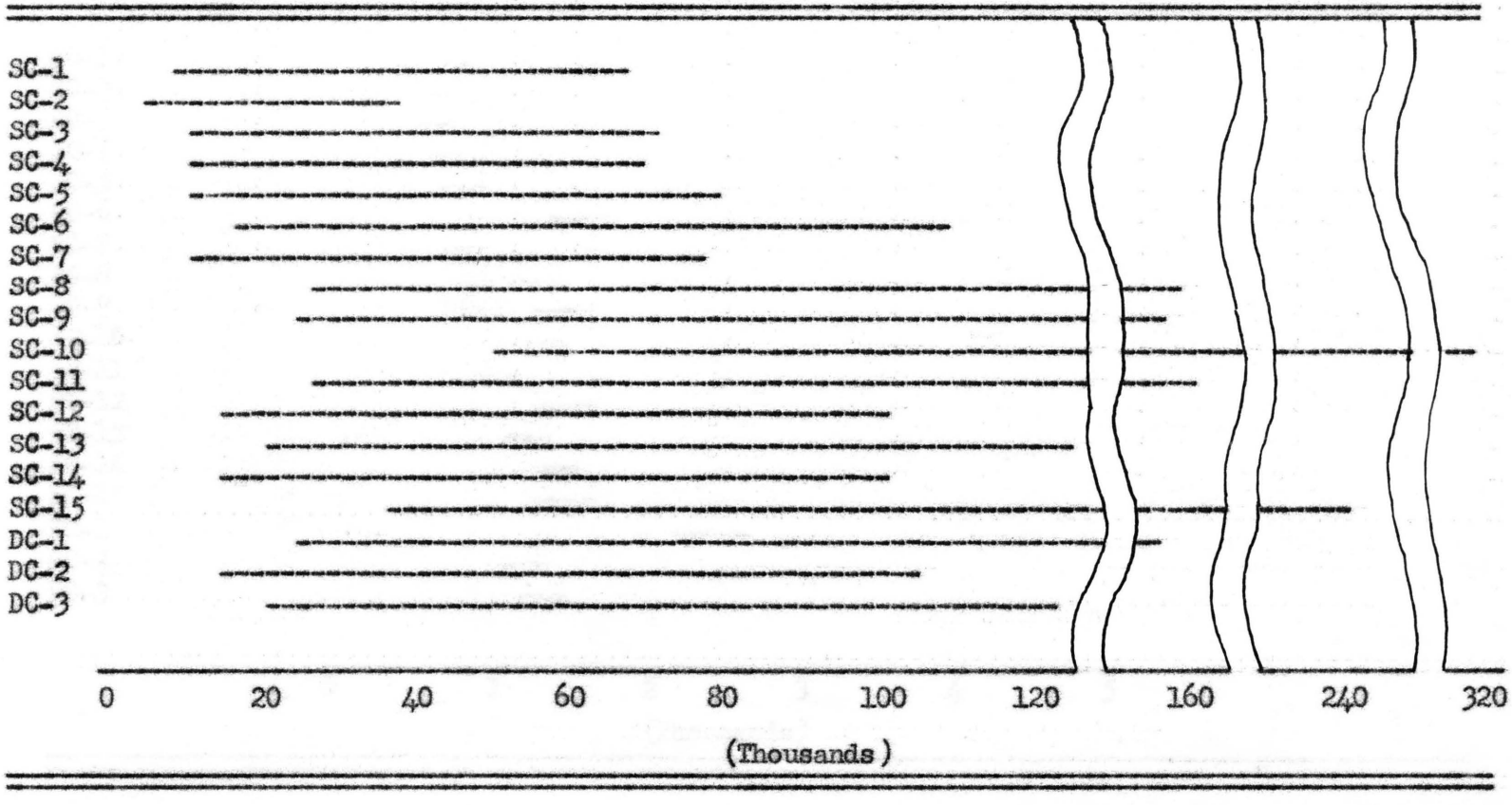
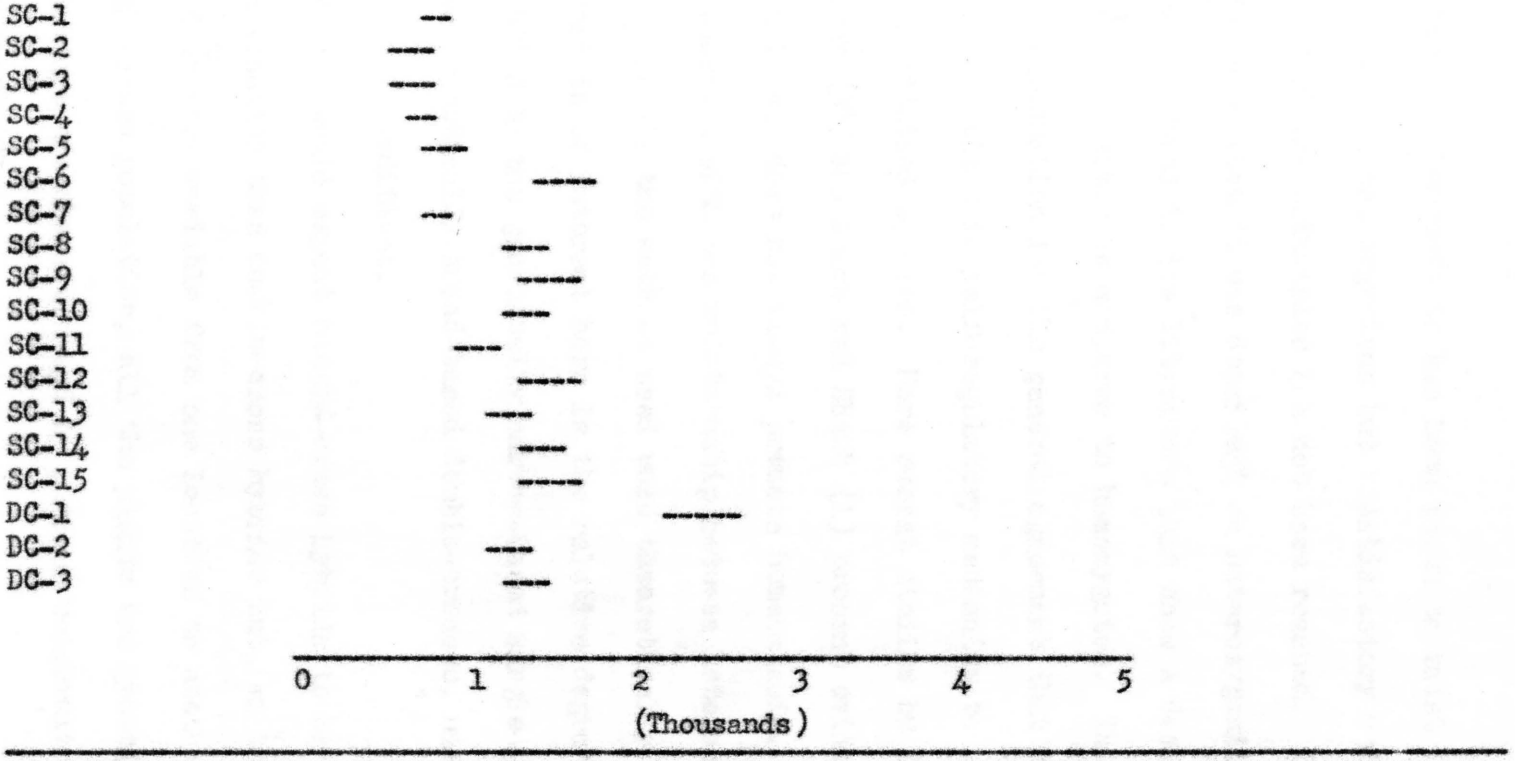


Figure 8. 1961-62 Ear Weight Within-Locations Confidence Intervals for Variance Estimates (5% Level).



DISCUSSION

The phenomenon of homeostasis has been shown to exist in varying degrees in biological organisms but a satisfactory understanding of its underlying principles has not been reached. Early workers tended to agree that it was dependent on heterozygosity and numerous examples are found in the literature that show a decreased variability for heterozygotes as compared to homozygotes. This could be a satisfactory explanation for the general agreement that cross-fertilized species exhibit this self-regulatory mechanism to a greater degree than self-fertilized species. More recent studies by Tebb and Thoday (34), Thoday (36) and Adams and Shank (1) present evidence that heterozygosity in itself does not always promote homeostasis. This problem is not concerned with the relationship between heterozygosity and homeostasis since all the entries used were theoretically 100% heterozygous. What is of interest here is the relative degree of homeostasis exhibited by the genetically narrow-based single-crosses as compared to the genetically broad-based double-crosses, under varying environmental conditions.

In theory, one would expect single-cross hybrids to be more uniform within a location than double-cross hybrids but, on the other hand, they should be more variable from one location to another.

In a single-cross population, all the plants are genetically the same and therefore are characterized by extreme uniformity in any one particular environment.

This genetic uniformity will also be a disadvantage if adverse environmental conditions are present since all the plants will be equally and uniformly affected. A relatively shorter pollination period (3 to 4 days) in a single-cross population, as compared to 5 to 8 days in a double-cross population, makes it susceptible to losses due to inadequate fertilization. By the time the last silks emerge from the tip of the ear, there may not be any viable pollen available. Other adverse environmental conditions such as lack of moisture, excess moisture, and high winds at some critical stage in the plant's development could drastically affect all the plants.

Plants in a double-cross population are more variable in most characteristics because of the presence of an infinite number of genotypes due to segregation of genetic materials in the $F_1 \times F_1$ cross. The increased genetic variability of double-cross hybrids tends to make them more homeostatic or better buffered against those unfavorable situations that frequently occur at one or more times during the growing season. A double-cross population will tend to be less uniform and may not take as full advantage of a highly favorable environment as a well-adapted single-cross. Such populations will tend to be more variable within any one environment but less variable from location-to-location because of the mixture of genotypes present. Theoretically, a double-cross population should have a higher mean value for yield when grown under different environments because of favorable environmental interactions by some of the genotypes in each location.

Comparisons of performance of single-crosses vs double-crosses of corn by Jones (19) and Sprague and Federer (31) tend to support the theories outlined above. They found that the average value of yield from single-crosses was more affected by variations in environment due to different locations or different years than the yield from double-crosses. The attainment of high average values for yield or a decrease in phenotypic variability over different environments may be considered indicative of better homeostatic properties of a population relative to other populations grown in the same environments.

In this study, flag leaf height and ear weight were the two traits measured. Previous work by Adams and Shank (1) included measurements of more characters but the two selected were considered to be adequate for this problem. Height would be a measurement of adaptive ability during the early part of the growing season while yield would be more influenced by environmental conditions during the latter part of the season.

This problem was designed to further investigate the relative homeostatic properties of single- and double-cross corn hybrids under Eastern South Dakota environmental conditions. This area is in the upper fringe of the Corn Belt and is characterized by relatively extreme climatic variations within one year or from year-to-year. As previously indicated, it was expected that the single-cross hybrids would show less variation within locations than the double-cross

hybrids because of the differences in genetic composition. On the other hand, the double-crosses were expected to show less variation between locations because of their theoretical superior homeostatic properties.

The use of six locations and, in the case of the second group of entries, two years should have provided a range of environments sufficient to test for differences in homeostasis between the entries and groups of entries. However, the locations, based primarily on soil type, and the years sampled in this study were limited. More accurate information on relative performance would require a long-time experiment to more adequately sample year-to-year climatic variations and a larger number of locations that varied not only in soil type, but also in fertility, structure, organic matter content, and the many other soil factors that influence plant growth.

Although the mean performance is of interest, it is not the important part of the picture, since the problem was not a yield trial but a study of differences in variability between the entries and between the groups of entries. The variability of an entry between locations and within locations should give an indication of the relative homeostatic properties inherent in that entry as compared to the other entries included in the test.

An analysis of variance could not be used since the underlying basic assumption that experimental errors have a common variance was not fulfilled in this problem. Various types of transformations are

available for removing heterogeneity of variance to make the means and variances independent. In this problem, the use of such a variance stabilizing transformation would not be desirable, even if it were possible, because of the genetic differences between the entries included in the tests. Since the assumption has been made that the population variance of an entry is an indication of its relative homeostatic properties, it would be undesirable to make the sample variances equal. Such an operation would eliminate the influence of the genotype on the variance and thus preclude making any comparisons and any conclusions as to differences of the homeostatic properties between the materials tested.

Comparisons were made between the relative homeostatic properties of the entries and classes of entries by the use of confidence intervals for the estimated variances. Some caution must be used in interpreting the results using this method.

The population variance is a constant and as such has no probability distribution while the sample variance will fluctuate since it is computed from randomly selected samples of the population. The proper interpretation of the 5% confidence interval is that 95% of the time this sample confidence interval will contain the true population variance. Comparisons between entries can be readily made by plotting the confidence intervals. An overlapping of confidence intervals of two or more entries indicates that there is no statistically significant difference in their variance at the level tested.

A comparison of the between-location confidence limits for plant height variance estimates showed no differences between groups of hybrids. Similar results were obtained when comparisons of ear weight variance estimates were made. There are two possible explanations for this lack of difference in variance. Either the entries had equal variance or the number of locations was not large enough to provide an adequate number of degrees of freedom to detect any real difference. The first explanation was invalidated when heterogeneity of error was detected. This indicates that the entries did have unequal variances. The second possibility is more logical and probably is the real cause. The number of locations and number of years were limited.

The within-location confidence limits for the variance give an indication of the variance of the entries under similar environmental conditions. One important thing to note is the difference in the scale and range of the confidence intervals. The between-location intervals are depicted in terms of thousands, ten thousands, and hundred thousands, while the within-locations intervals are in terms of tens, hundreds, and thousands. This is to be expected since the environmental fluctuations within a location would be much smaller than those between locations.

The 1960 within-location variance estimate confidence interval data does not show any differences or even any trends of differences between the entries or between the single- and double-cross groups.

In addition to the two possible explanations mentioned previously, a third one is present here. The entries used are all more-or-less adapted to this area so any great differences in plant height or ear weight would not be expected.

The first and only differences were found in the 1961-62 within-locations variance estimate confidence intervals. Comparisons of the confidence intervals for plant height show that, with one exception, the single-crosses had a significantly lower variance than the double-crosses. The differences in ear weight confidence intervals were not as definite. Six of the single-crosses were significantly lower. The high confidence intervals for eight other single-crosses may be due to the genotype of one or both of its inbred parents.

During the harvesting operation, no notation was made as to the number of ears on individual plants. In some cases two ears were present, so they both were harvested, weighed together and recorded as ear weight for that plant. This is a possible source of the increase in the variance for some of the single-crosses. Recent unpublished data by Shank shows that single-crosses with B8, Il53RM, or Oh56A as one or both of the parents tend to have a relatively large number of plants with two ears. Comparisons of ear weight of single-eared plants with the total ear-weight of two-eared plants show an extremely wide range in ear weight per plant. In most cases, the combined weight of two ears was approximately fifty grams larger

the weight of a single ear but some cases were noted where there was no difference.

The use of single-crosses which varied in their ability to produce double ears is a very likely source of some of the variability in the fifteen single-crosses. Of the nine single-crosses which had the highest variance in ear weight, eight had B8, Il53RM, or Oh56A as a parent.

A possible way to prevent this increased variation from entering into tests would be to make an attempt to sample only certain plants. A decision could be made prior to sampling as to what type (single- or double-eared) were to be included and only plants of the type desired should be sampled. In practice, this may not work because this condition is apparently due to an environment-genotype interaction since it is sporadic in its occurrence. A particular single-cross may have a majority of single-eared plants in one location or one year, while the double-eared plants may be predominant in other instances. Further studies along this line are needed to develop procedures for properly sampling populations that are variable for this characteristic.

The comparisons of the 1960 plant height and ear weight means and grand means show that the average yield generally was not significantly different between single-crosses and double-crosses. This is what one would expect, since all the crosses are more or less adapted to this area. A comparison of the plant height means of each entry

at each location show that two single-crosses excelled at each of two locations and that two different single-crosses had the highest value in the other two locations. Ear weight means by location show one single-cross highest in four locations and one double-cross highest in the remaining two locations. There was something of a trend here, but not complete agreement with the commonly accepted idea, first proposed by Jones (19), that the highest yields are produced by a single-cross. The single-crosses vary more in mean values from location-to-location and from year-to-year and usually it is a different one that excels in each location. This is indicative of the relatively poorer homeostatic properties of single-crosses as compared to double-crosses.

The 1961-62 data did not indicate such a trend. Single-crosses as a group tended to exhibit the highest mean values for plant height and ear weight at the different locations. The plant height mean values were quite variable and wide ranges of significant differences for plant height were found when the entries were compared. Ear weight mean differences were less pronounced as evidenced by fewer significant differences. The increase of significant differences is due to the more diverse genotypes involved. As a group, these entries are not as well adapted to this area as the hybrids used in 1960.

Comparisons of grand means by use of Duncan's new multiple range test is not completely valid because of the presence of

heterogeneity of variance in the tests. Its use is justified in that it is the best approximate test available for making comparisons of this type. The mean performance of the entries or classes of entries was not the primary objective of the problem.

The choice of single-and double-cross entries that were used in this series of tests leaves much to be desired if one wants to use the results obtained to make blanket recommendations for or against the use of single-cross hybrids in this area of South Dakota. Further research in this area should include commercial single-crosses that are available to farmers, as well as experimental single-crosses that have demonstrated their yielding ability in prior tests. However, due to the number of locations and/or years required to detect the relative differences in variability, it does not appear feasible to gain further information in this area.

Commercial single-cross seed has been sold in the Brookings area of South Dakota for the past two or three years and no widespread adverse reports have been made on their performance. It should be noted, however, that the past few years have been relatively favorable for corn production so that the single-crosses may not have been exposed to any great stresses due to environmental conditions. The apparent acceptance of single-crosses in certain areas of South Dakota will no doubt encourage the commercial seed companies to include some of their better single-crosses in the state corn performance yield trials. This is perhaps the logical way to properly

study this problem in order to obtain results that will have practical applications in making further recommendations as to the use of single-cross hybrid corn.

SUMMARY

This study was concerned with testing the hypothesis that single-cross hybrids have relatively poorer homeostatic properties as compared to double-cross hybrids when grown under diverse environmental conditions. Two groups of hybrids were grown at six locations over a three year period. Measurements were taken of plant height and ear weight and used to compute means and variances for each entry. The presence of heterogeneity of variance precluded use of analysis of variance calculations. A transformation was not considered desirable because it would prevent detection of differences in variability between entries. The variability of an entry was considered to be an indication of the homeostatic properties of that entry relative to other entries grown in the same environments.

Comparisons between entries were made by computation of confidence intervals for the variance estimate for each entry by use of the chi-square method. Overlapping of the confidence intervals of two or more entries was considered to be indicative of no significant differences in variability between the entries compared.

The hypothesis that single-cross hybrids have a higher between-location variance and double-cross hybrids a higher within-location variance was supported to a certain extent by this study. The differences were most evident in the 1961-62 plant height within-locations variance and to a lesser extent in the 1961-62 ear weight within-locations variance.

Plant height and ear weight means were compared and general support for the theory that a single-cross usually has the highest value in any one location was found.

The hybrid entries used were not all varieties that are grown for grain production in this area. Further investigations in this area should include commercial single- and double-crosses if recommendations are to be made for or against the use of single-cross hybrid corn in Eastern South Dakota.

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